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## The effects of diet on herbivory by a predaceous lady beetle

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We hypothesize that herbivory by predators is affected by the complexity of their diet. *Coleomegilla maculata* larvae fed prey – *Acyrtosiphon pisum* or *Ostrinia nubilalis* eggs – consumed two to three times more plant tissue (pinto beans) than those fed a mixed diet (containing pollen substitute and prey-based components). Simple, prey-only diets appear to lack plant-based nutrients important to this predator.

**Keywords:** Coccinellidae; *Coleomegilla maculata*; facultative phytophagy; nutrition; predation; omnivory

Many coccinellids consume fungi, pollen, nectar, and plant tissue in addition to arthropod prey (Lundgren 2009a). These non-prey foods seldom support successful development and reproduction in coccinellids (Evans, Stevenson, and Richards 1999; Berkvens et al. 2008), and it is often erroneously concluded that they serve only to sustain predators until prey become available (Lundgren 2009b). It is important to recognize that these non-prey foods contain different nutrients from prey, and predators fed mixed diets often have higher fitness than those fed simple prey-only diets (Lundgren 2009a). Under field conditions predaceous coccinellids regularly consume non-prey foods even when prey are widely available, indicating that these foods may help to complement prey-only diets (Triltsch 1999; Weber and Lundgren 2009; Berkvens et al. 2010; Davidson and Evans 2010). *Coleomegilla maculata* DeGeer and *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), both relatively polyphagous species, consume foliage of maize (*Zea mays* L.) under laboratory conditions (Moser, Harwood, and Obrycki 2008; Moser and Obrycki 2009). Here, we test the hypothesis that *C. maculata* is more likely to consume plant tissue when they are reared on prey-only diets than when they are fed mixed diets.

*Coleomegilla maculata* adults originated in Beltsville, MD, and were reared continuously for more than five generations. Neonates were randomly assigned to one of three dietary treatments (housed in 4-cm diameter plastic Petri dishes), that received (1) excess *Acyrtosiphon pisum* (Harris) (Hemiptera: Aphididae) ( $n = 32$ ), (2) egg masses of *Ostrinia nubilalis* Hübner (Lepidoptera: Crambidae) ( $n = 34$ ), or (3) Lundgren's Super C MAC Diet ( $n = 35$ ). *Acyrtosiphon pisum* were reared on *Pisum*

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*sativum* L. *Ostrinia nubilalis* egg masses were produced by the USDA-ARS laboratory in Ames, IA and were frozen until use. *Lundgren's Super C MAC Diet* consists by volume of five parts Bee-Pro<sup>®</sup> pollen substitute (Mann Lake Ltd, MN, USA), three parts tropical fish flakes (TetraColor<sup>™</sup> tropical fish flakes, Tetra Holding Inc., Blacksburg, VA, USA), three parts cichlid pellets (Omega One cichlid pellets, OmegaSea, Ltd, Sitka, AK, USA), three parts sun-dried *Gammarus pulex* (L.) (Amphipoda: Gammaridae) (Tetra BabyShrimp, Tetra Holding Inc.), and two parts *Ephestia kuehniella* eggs (Beneficial Insectary, Redding, CA, USA). All components (aside from the eggs) were pulverized prior to mixing the diet. Larvae received water as a saturated cotton wick. Diet was changed daily, and Petri dishes were replaced every 48 h. Rearing conditions were 28°C, 16 h L:8 h D photoperiod and approximately 40% relative humidity.

Survival and the duration of each larval stadium were recorded for each individual daily for 9 d. At this point larvae were weighed and transferred to plant tissue with forceps. Pinto beans (*Phaseolus vulgaris* L.) were grown to the two-leaf stage under controlled environmental conditions ( $24 \pm 0.1^\circ\text{C}$ , 16 h L:8 h D, 75% RH) in a potting mix (Sungro Sunshine SB300 Universal Professional Growing Mix; Sungro Horticultural Products, Bellevue, WA, USA) and were watered daily for approximately 14 d. Plants were removed from the soil, and soil was washed from the root mass prior to inserting it into a water-filled 50 ml centrifuge tube covered in Parafilm. The plant and tube were then placed into a 710 ml plastic cup with a larva, and sealed with mesh clot. After 24 h, tissue damage from the plant was photographed using a zoom stereomicroscope (Model SMZ1000, Nikon Instruments Inc., Melville, NY, USA). The digital image files were exported to ImageJ (U.S. National Institutes of Health, Bethesda, MD, USA, <http://rsb.info.nih.gov/ij/>), converted to 8-bit grayscale, and the 2-D leaf area consumed by each larva was calculated.

The durations of the first, second, and third stadia were compared among treatments using ANOVA, and significantly different treatment means were separated using the LSD means separations. Mean larval mass just before they were offered the bean tissue was compared among the treatments using ANOVA and LSD means separations. The mean area of plant tissue consumed (standardized according to larval size) was compared among the treatments using Kruskal–Wallis non-parametric ANOVA, and significantly different means were separated using K-W ANOVA pairwise comparisons. Statistics were run on Systat 11 (Systat Software Inc., Chicago, IL, USA).

Although all were of high quality, the three diets tested supported larval development to different degrees. First instars fed diet developed significantly faster than those fed eggs, and aphid-fed first instars developed at a significantly distinct intermediate rate ( $F_{2, 95} = 6.60$ ,  $P = 0.002$ ). Aphid-fed second instars developed significantly faster than egg-fed second instars, and those fed diet had a significantly distinct intermediate developmental rate ( $F_{2, 94} = 3.11$ ,  $P = 0.049$ ). Diet-fed third instars developed significantly more slowly than the prey fed treatments, which were statistically similar ( $F_{2, 58} = 14.22$ ,  $P < 0.001$ ). The result of these differences in growth rates is that 87, 67, and 67% of aphid-, diet-, and egg-fed treatments were 4<sup>th</sup> instars at the end of the experiment. Larvae reared on diet, aphids, and eggs weighed a mean (SEM) of  $8.14 \pm 0.54$ ,  $7.72 \pm 0.34$ , and  $5.86 \pm 0.31$  mg each ( $F_{2, 95} = 8.82$ ,  $P < 0.001$ ). Arthropod prey vary widely in their suitability for developing predators

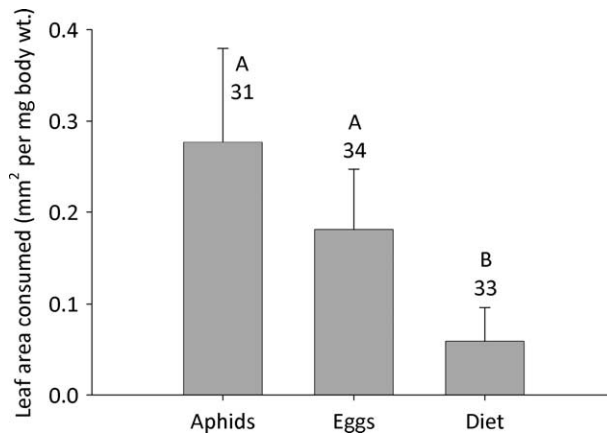


Figure 1. The mean ( $\pm$ SEM) leaf area (standardized by body weight) consumed by *Coleomegilla maculata* larvae reared on aphids (*Acyrtosiphon pisum*), eggs (*Ostrinia nubilalis*), or a mixed diet containing prey and non-prey components. Numbers above the bars refer to sample sizes, and bars capped with different letters refer to significantly different means (non-parametric pairwise comparisons;  $\alpha = 0.05$ ).

(Michaud 2005; Omkar, Kumar, and Sahu 2009), and more complex (or mixed) diets are often superior to those composed of solitary components in supporting predator development and fitness (Lundgren 2009a). This is in part because the defensive characteristics and nutritional quality of prey often vary, and arthropods self-select their diets to obtain optimal nutrient ratios when given the option (Waldbauer and Friedman 1991).

The diet of *C. maculata* larvae affects their likelihood to consume plant tissue, and those fed prey-only diets consumed two to three times more plant material than those fed a mixed diet. Larvae reared on aphids or eggs ate significantly more plant area for their body size than those reared on the customized mixed diet (Kruskal–Wallis  $\chi^2 = 10.36$ ,  $df = 2$ ,  $P = 0.006$ ) (Figure 1). The mean (SEM) area of plant tissue consumed was  $1.74 \pm 0.66$ ,  $1.08 \pm 0.40$  and  $0.44 \pm 0.32$  mm<sup>2</sup> for aphid-, egg-, and diet-fed treatments. Plant tissue may contain nutrients that are deficient in prey, and may be critical for the optimal growth and performance of predatory insects (Lundgren 2009b). Increased consumption of plant material by prey-fed larvae is consistent with the hypothesis that plant tissue provides critical nutrition that is lacking in many simple, prey-only diets. Also, this result suggests that predator larvae compensate for this deficiency by consuming additional plant tissue. This omnivory is particularly important in light of the current use of plant-incorporated insecticides in agroecosystems, which may inadvertently expose plant-feeding predators to toxins.

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